Evolution of social behavior

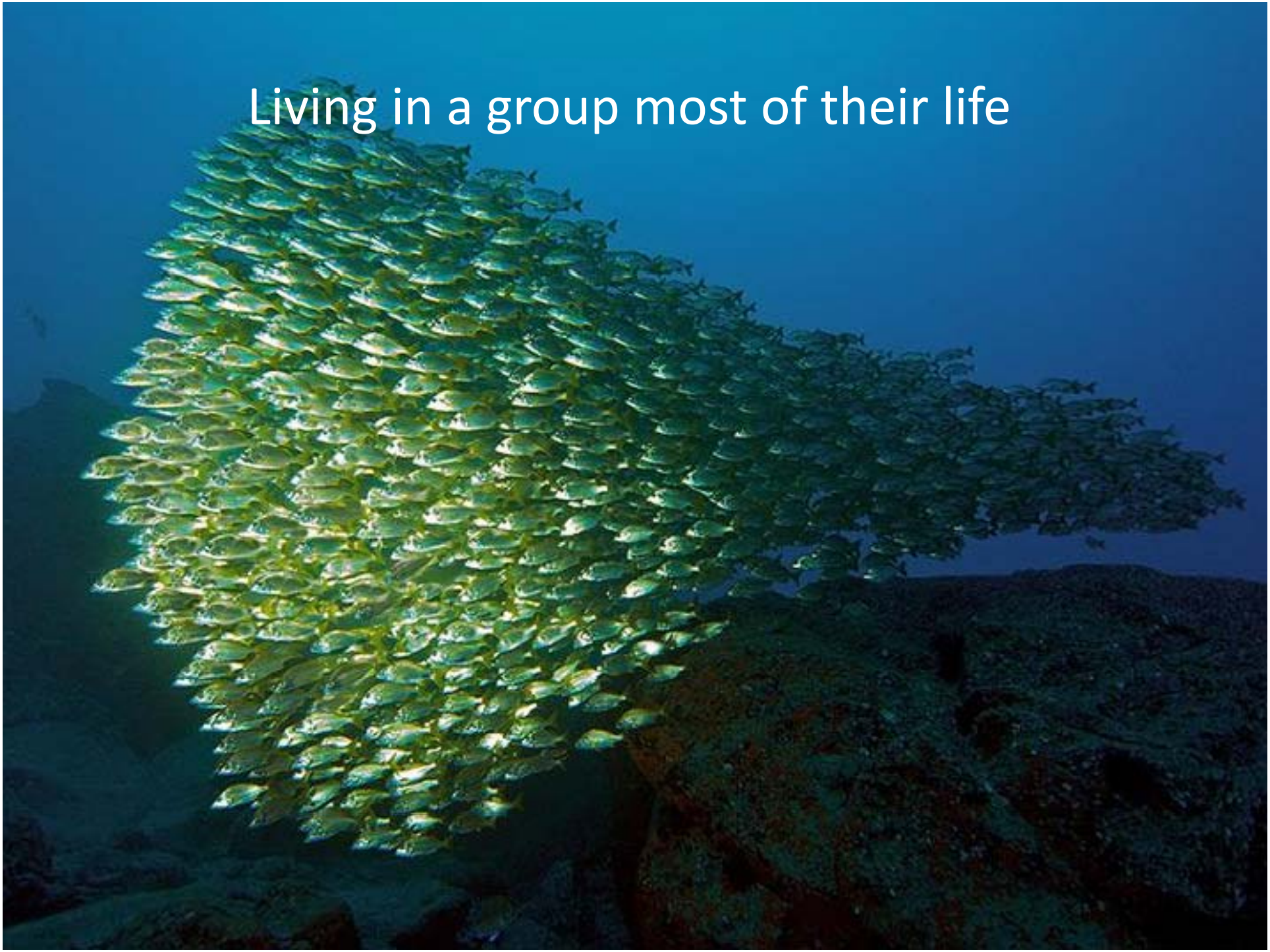
Social behavior:

Inter-individual relationships among the members of that population.

- solitary, pair-bond, family, colonial, aggregation/ schooling


Solitary most of its life

Sexual difference in social structure


Living in a group most of their life


Black-capped chickade

Seasonal difference in social structure

Black-capped chickadees

Summer: territorial, pair-bond

Winter: social flock-hierarchy

Some species are more social than others?

How ?(proximate causes)

Some species are more social than others?

Why ?(ultimate causes)

More social means more adaptive?

More social means more adaptive?
No, not really.

Natural selection assumes that behaviors evolved to best adaptive to species-specific ecological environment.

Species-specific adaptation of social behavior

The benefit and cost of social life

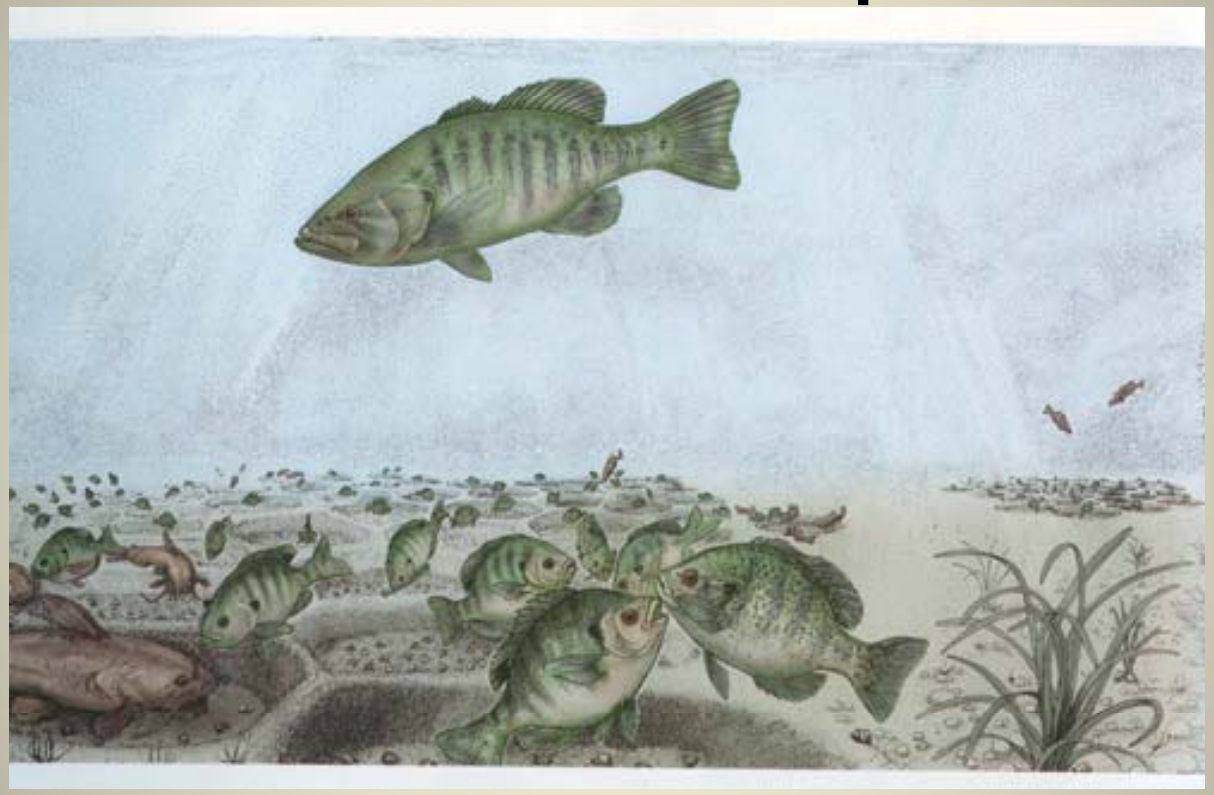
Cost: compete for resources; parasites/diseases

Benefit: foraging, anti-predator, helper

The benefit of social life

Benefit: foraging, anti-predator, helper..

Benefit of living in a group: Mutual defense of predator



Bluegills

The cost of social life

Effect of parasites on cliff swallow nestlings

Which nestling suffers from parasite infection?

Parasites (fly larvae) in cowbird nestlings

Until mid-1960s, biologists took helpful behavior for granted because they assumed that animals should assist one another for the benefit of the species as a whole (one should help each other)

Group selection ?

Helpful behavior

How does it evolve
through natural selection?
(benefit > cost)

Individual/ group/ genes as unit
of selection?

But, does group selection work?

Lemmings (rodents)

Extreme population fluctuation

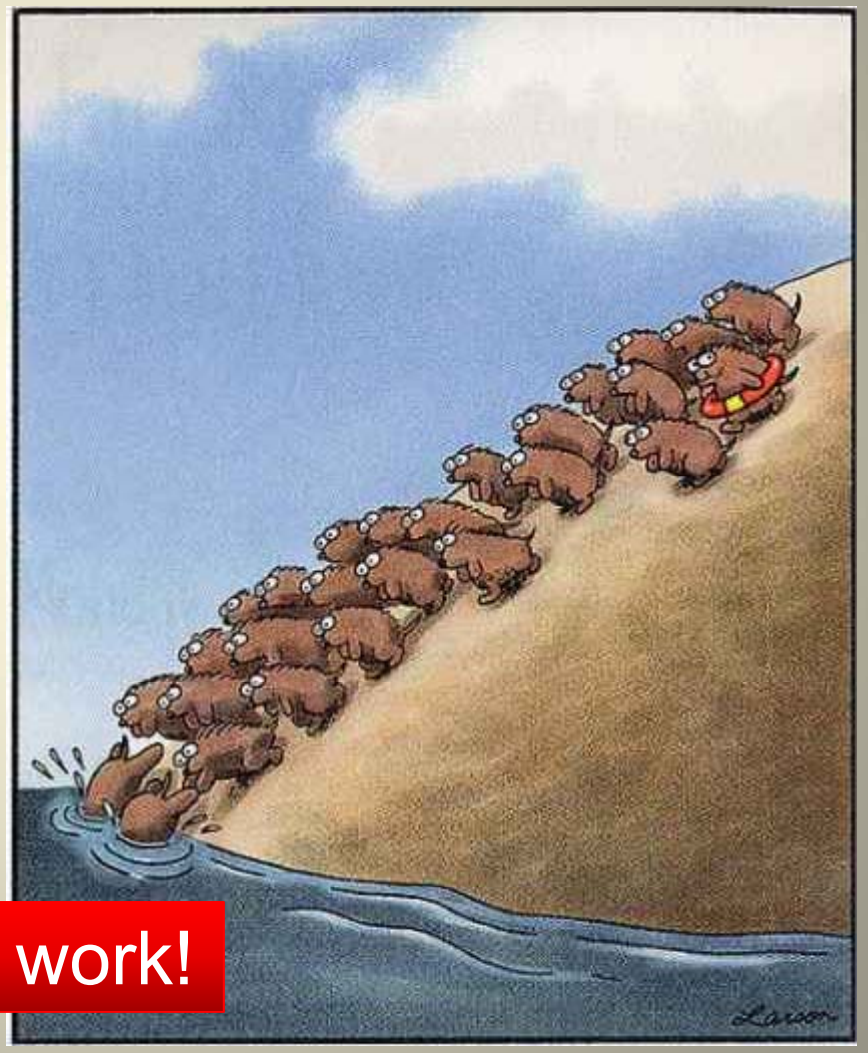
High population density →

→ migration → many died

→commit suicide to control population size, for the benefit of lemming species?

Cheaters will have reproductive success, And their “cheating” genes will prevail!

Lemmings (rodents)



Group selection doesn’t work!

Mating behavior of praying mantis

Types of social interactions

1. Mutualism (cooperation)
2. Reciprocal altruism
3. Altruism
4. Selfish behavior
5. Spiteful behavior

1. Mutualism

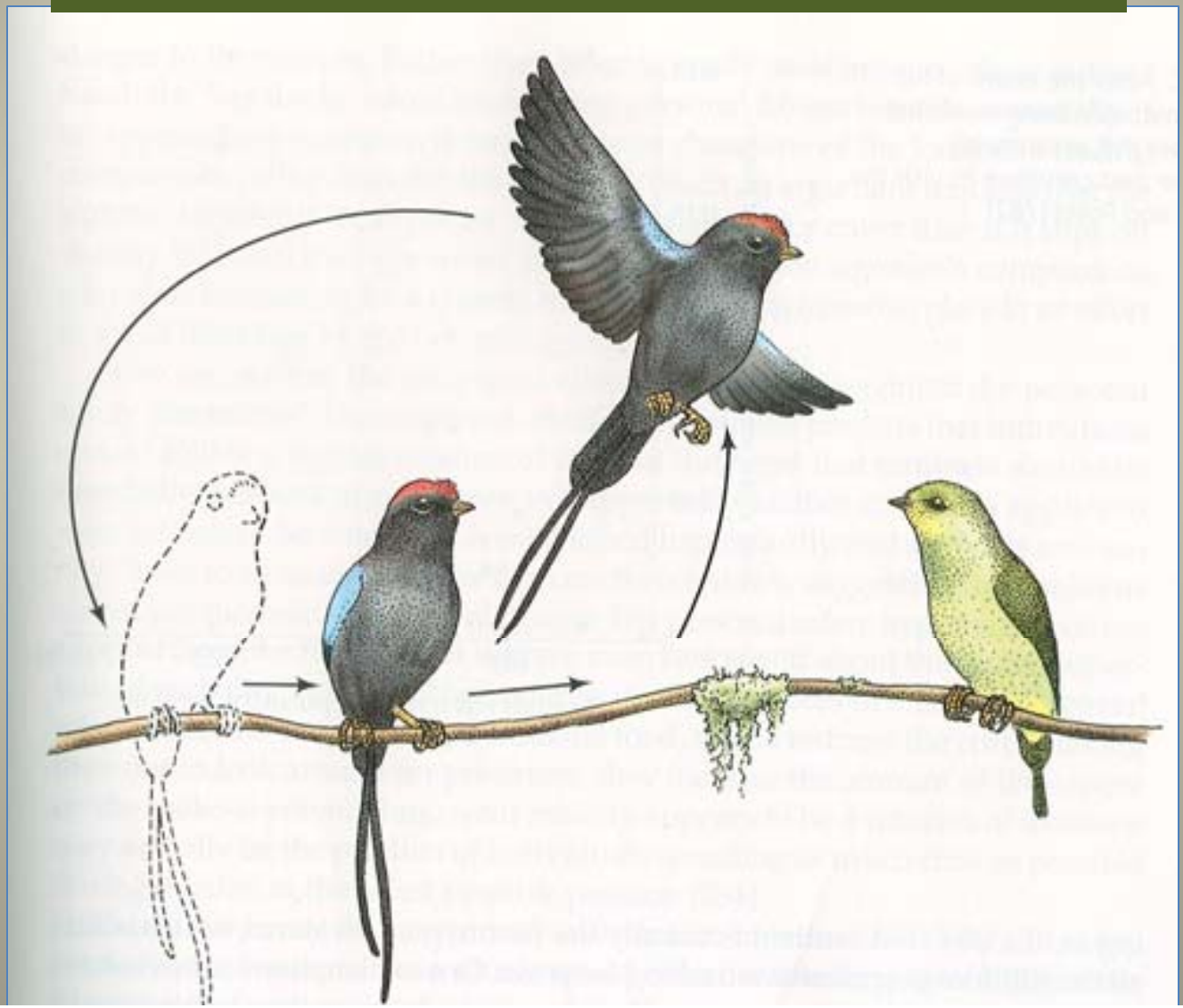
Helper (gain); recipient (gain)

Both helper and recipient have reproductive gains from their interaction.

Examples?


Cooperative courtship of
the long-tailed manakin

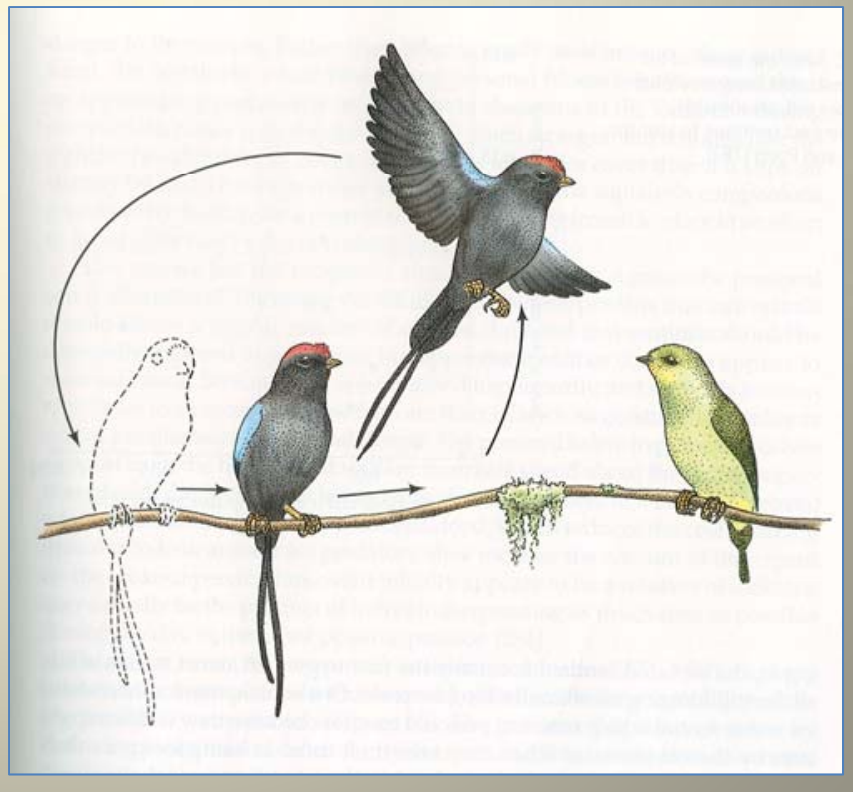
Cooperative courtship of the long-tailed manakin



Cooperative courtship: long-tailed manakin

Cooperative courtship of the long-tailed manakin

One is dominant, the other is subordinate.



Why does the subordinate help?

--increase the mating chance

Types of social interactions

1. Mutualism (cooperation)
2. Reciprocity
3. Altruism
4. Selfish behavior
5. Spiteful behavior

2. Reciprocity

Social grooming

2. Reciprocity

Helper (gain-delayed); recipient (gain)

Both helper and recipient have reproductive gains from their interaction, but helper's gain will be delayed.

2. Reciprocity

-- Game theory --

An animal's behavior is based on the other's action.

Example: Prisoners' dilemma

2. Reciprocity-prisoners' dilemma

		Player B: Cooperate	Player B: Defect
Player A	Cooperate	Reward for mutual cooperation	Maximum punishment
Player A	Defect	Maximum reward	Punishment for Mutual defection

Let's play the game!

1. play one time only with a stranger….
   *what strategy will you gain most?
2. play 10 times with someone you know…
   *what strategy will you gain most

"The Prisoner's Dilemma"		Individual #2	
		Cooperate	Defect
Individual #1	Cooperate	(3,3)	(0,5)
	Defect	(5,0)	(1,1)

Prisoner's dilemma

Payoffs for player's response ranks….

1. Defect while other players cooperate
2. Both cooperate
3. Both defect
4. Cooperate while other player defects

Optimal response: always defect, never cooperate

Reciprocity should never evolve?

It could, if two players interact repeatedly.

For reciprocal altruism to work as a strategy, several conditions are required:

1. Frequent interaction (play >1 game)
2. Recognizing individuals
3. Remembering past interactions with individuals
4. Assisting only those who provided past assistance

“ tit for tat” strategy

(reciprocity strategy based on prisoner’s dilemma)

Tit for tat strategy

An individual cooperates on the initial encounter with a partner subsequently copies its partner's pervious move.

1. If the partner cooperates, then cooperate.
2. If the partner defects, then defects.

Tit for tat strategy

Three fundamental characteristics

(1) Nice: never cheats first

(2) Retaliatory: always responds to a partner that is cheating.

(3) Forgiving: only remembers one move back in time.

Coalition of male olive baboons

Tit for tat strategy in animals

Food sharing in blood-sucking vampire bats

Female bats regurgitate blood meals to others that failed to obtain food

Food sharing "tit for tat" in blood-sucking vampire bats

1. Bats that can recognize one another are more likely to give blood to those that have donated blood to them in the past (reciprocate)

2. Blood sharing is a huge benefit for recipient but not a big cost for donor.

Prisoner's dilemma and Tit for tat strategy

- In a one-time game, you should defect because the average payoff is greater.
- If the game is to be repeated many times, it is in both player's long-term interest to cooperate.
- Tit-for-tat is an evolutionarily stable strategy, or solution, to a repeated Prisoner's Dilemma game. The rule is: cooperate on the first play and then do what your opponent did in the last play.

Decision making “tit for tat” in humans

		Player B	
		Cooperate	Defect
Player A	Cooperate	Reward for mutual cooperation	Maximum punishment
	Defect	Maximum reward	Punishment for Mutual defection

Playing "Tit for tat" in the fMRI (monitoring brain activity)

1.Most emotionally rewarding payoff is "both cooperate" (induce highest neural activity in brain's reward areas);

even though the most monetary reward is to "cheat"

2. Subjects derived pleasure from punishing cheaters (induce high neural activity in reward area when punish the cheater).

3. When subjects mutually trust, oxytocin increases.

Types of social interactions

1. Mutualism (cooperation)
2. Reciprocity
3. Altruism
4. Selfish behavior
5. Spiteful behavior

3. Altruism

Helper (lose); recipient (gain)

Donor (helper) really does permanently lose opportunities to reproduce as a result of helping another produce more surviving offspring.

--reduce individual's reproductive success

The Conundrum of Altruism

- **Selfish and mutualistic acts increase the fitness of the actor. It is clear that these behaviors will be selected for by natural selection, because those who act selfishly or mutualisticly derive a direct/immediate benefit from their action.**
- **Altruism is a problem to explain because by definition it decreases the fitness of the individual performing the behavior while increasing the fitness of a competitor (the recipient) and therefore reduces the contribution of the genes that underpin that behavior to the next generation.**
- **Even spiteful interactions can be explained by natural selection as long at the recipient pays a greater fitness cost than the actor.**

How can altruism ever evolve?

1. Group selection?

2. Indirect selection (Kin selection)
   (W. D. Hamilton: kinship theory)

Halmilton's kinship theory - inclusive fitness -

* **Inclusive fitness**: an individual's total fitness is based on the number of its own offspring and the contribution it makes to the reproductive success of its genetic relatives.

* include both direct fitness (your own offspring) and indirect fitness (your sib's offspring, your grandchildren).

How to calculate indirect fitness?

Two siblings are related to one another by **r=0.5**

Sibling #1 has gene X, 50% (0-100%) chance she received gene X from her mom.

Sibling #2 has gene X, 50% (0-100%) chance she received gene X from her mom.

There is 25% chance (50%x50%) that the siblings share gene X through their mother.

There is 25% chance that the siblings share gene X through their father.

The chance that the siblings share gene X through either their mother or father: 25% + 25% =50%

The chance that the siblings share gene X through the parents =50% r (**relatedness)** =0.5

Quiz :

The genetic relatedness between cousins: r = ?

The genetic relatedness between grandparents and grandchild: r = ?

Hamilton's Kin selection:

Hamilton's (1964) theory of kin selection predicts that altruistic behaviors will be favored by selection if the costs of performing the behavior are less than the benefits to the receiver discounted by the relatedness between actor and recipient.

Hamilton's rule:

$$c < rb$$

c = cost of the helper
b = benefit to the recipient
r = relatedness between helper and recipient

Calculate inclusive fitness

Direct fitness: N1 survive because of parental care (individual produces offspring)

Indirect fitness: N2 survive because of help (individual helps relatives)

Direct fitness: N1 x r

Indirect fitness: N2 x r

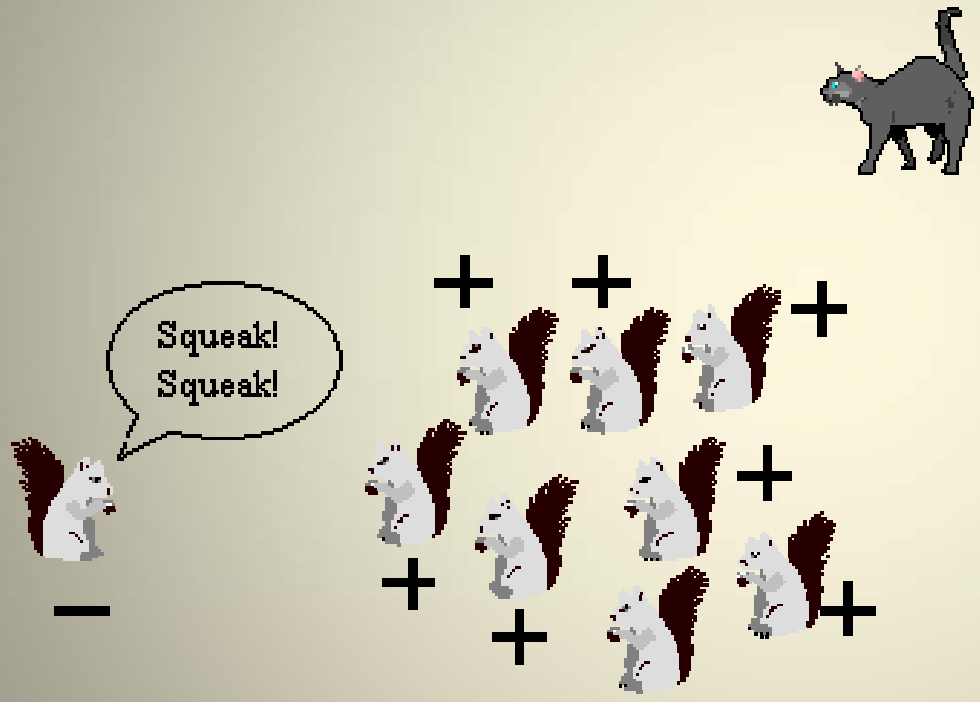
Why do ground squirrels produce alarm calls, sometimes?

Altruism and Warning Calls

Gives a warning call
(ACTS ALTRUISTICALLY)

Doesn’t give a call (ACT SELFISHLY)

Giving the warning call and accounting for kin selection where the cost of giving the call is .3 and the benefit .1 to each of the others and the actor is the sister of the others (r = .5)



c = .3

b = .1 x 8 = .8

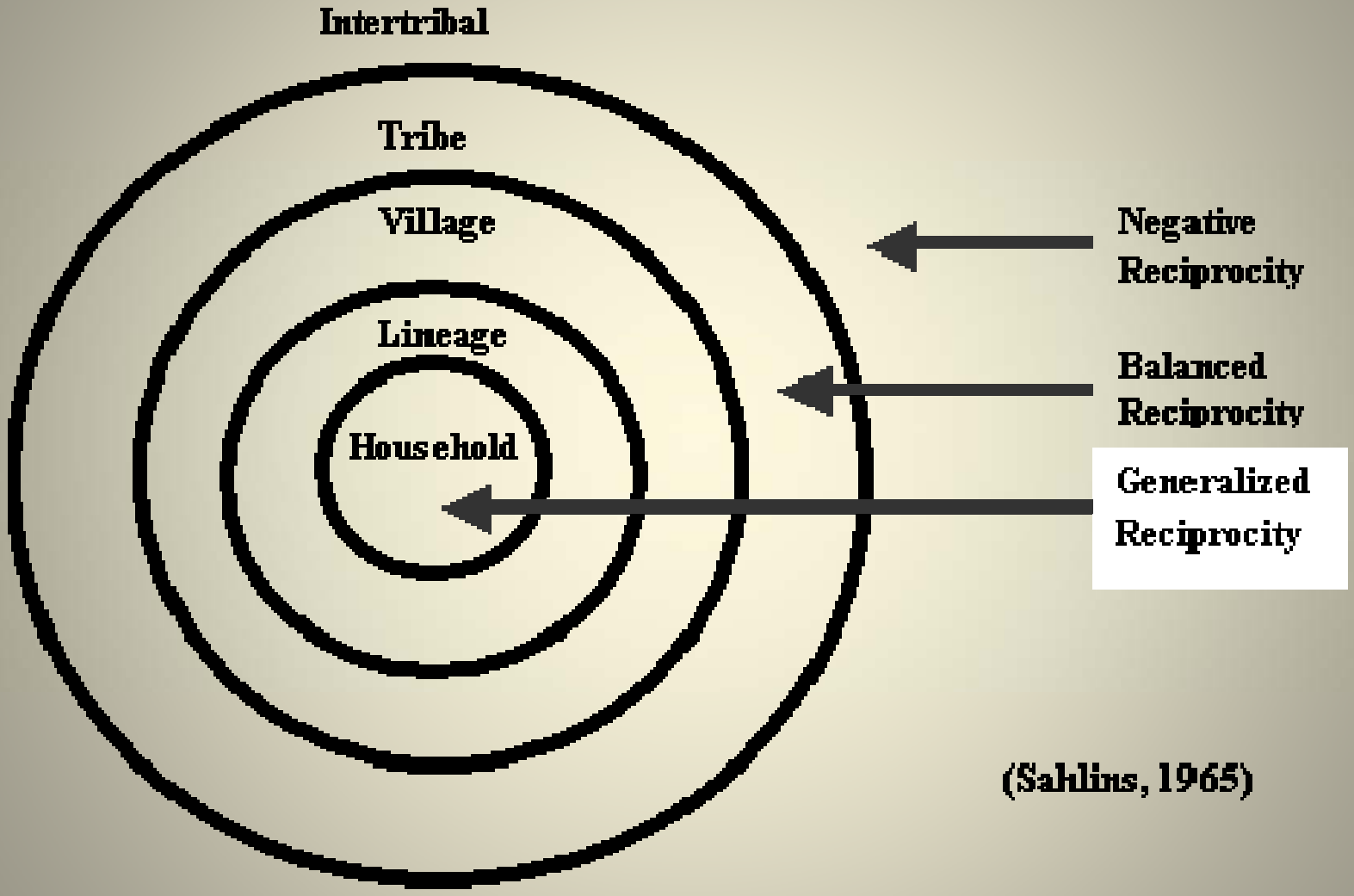
r = .5

rb = .5 x .8 = .4

Give the warning call because c<rb (.3 < .4)

- **Kin selection is a powerful motivation for cooperation in social interactions.**
- **Kinship is an important principle for the organization social structures**
- **In humans, tribal and band societies kinship is the primary principle around which groups form and is primary in defining the relationships between groups.**

Spheres of Interaction and Exchange



(Sahlins, 1965)

Example of altruistic behavior in animals?

Pied kingfisher

Altruism in Pied kingfisher

1. Nest colonially → social
2. Some males are unable to find a mate
   become primary helper, help their mom and nestlings (siblings)
3. Some males become secondary helper, help non-relatives
4. Some males sit out and wait for next year-- delayer
3. Many males find a mate next year and have their offspring.

What strategy is the best (max benefit/ cost)?

Primary helper: benefit/ cost?
Secondary helper: benefit/ cost?
Delayer (non-helper): benefit/ cost?

Altruism in Pied kingfisher

The benefit and cost of helping behavior what behavioral strategy is the best?

	Young r f1 First year	O r s m f2 Second year (paired)
Primary helper	1.8 x 0.32 = 0.58	2.5 x 0.50 x 0.54 x 0.60 = 0.41
Secondary helper	1.3 x 0.00 = 0.00	2.5 x 0.50 x 0.74 x 0.91 = 0.84
Delayer	0.0 x 0.00 = 0.00	2.5 x 0.50 x 0.70 x 0.33 = 0.29

O= offspring; **s** = p of survival to next year; **m**= p of finding a mate in the second year

Altruism in Pied kingfisher

Why helping non-relatives?

Ecological constraints:

--availability of limited territory

--availability of females

Helping can better access the resources

How to test this hypothesis?

Summary

Evolution of Helper's altruism

1. Inclusive fitness $C < {}^{*}b \times r$

2. Ecological constraints.
   (helpers to stay or disperse depends on resources)

Benefit or cost?

Outcome	Actor	Recipient
Mutualism	+	+
Reciprocity	+ (delay)	+
Altruism	- (direct)	+
Selfish	+	-
Spiteful	-	-

The evolution of eusocial behavior

What is eusocial behavior?

A form of social organization characterized by:

1. Adults live in a group.
2. Cooperative care of juveniles
3. Labor division
4. Overlap in generations

1. Adults live in a group.
2. Cooperative care of juveniles (even not their own)
1. Labor division (some are sterile)
2. Overlap in generations

What species are eusocial?

Arthropoda				
	Class: Insecta			
		Orders:		
		Isoptera		All eusocial, many advanced
		Hemiptera		~50 sp eusocial
		Thysanoptera		~6 sp eusocial
		Coleoptera		1 species "Ambrosia beetle"
		Hymenoptera		
			Ants	All species (except a few highly derived species) ~14000
			Bees	Only 300-400 of ~ 4000 sp are eusocial
			Wasps	Most are not social, ~900 species are eusocial
	Subphylum: Crustaceae			
		Snapping shrimp		*Synalpheus*
Chordata				
	Class: Mammalia			10's of primitively eusocial species
		Family: Bathyergidae (African mole rats)		2 advanced eusocial species: naked mole rat (*Heterocephalus glaber*), Damaraland mole rat (*Cryptomys damarensis*)

Social aphid

Why eusocial?

What is the advantage of living in a group?


1. Group Defense

2. Foraging

Mutualism between leaf cutter ants and fungus

Many eusocial species:

Reproductive division of labor evolves from sterile castes which often have helping behavior (female workers).

Why they sacrifice their own reproductive success to help others?

How did Eusociality evolve?

Darwin (1859) commented on the challenge of understanding eusociality as "one special difficulty, which at first appeared to me insuperable, and actually fatal to the whole theory…”

How did Eusociality evolve?

1. Kin selection by haplodiploid, r ↑
2. Kin selection by inbreeding, r ↑
3. Ecological (resource) constrains
4. Combination of 1-3.

Many eusocial species:

Reproductive division of labor evolves from sterile castes which often have helping behavior (female workers).

Why they sacrifice their own reproductive success to help others? -altruism

Hamilton's rule: altruism can evolve if:

$$*C \times r_c < *b \times r_b$$

If the relatedness of the altruist to the relatives it helps (r_b) is particularly high, then indirect fitness would be increased.

True in many eusocial insects !

Many eusocial insects are haploidiploid

In bees, ants and wasps (haploidiploid species)

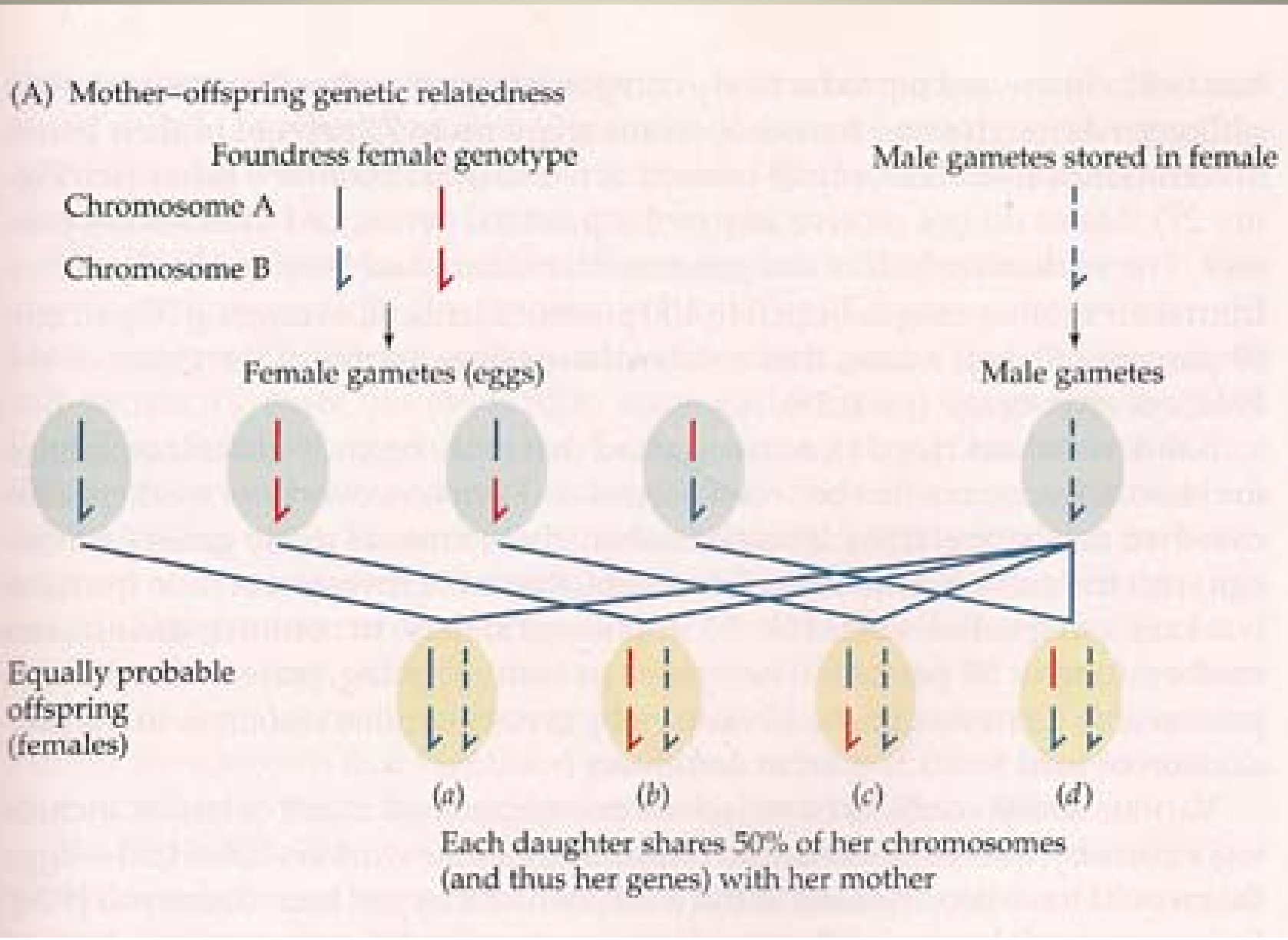
Males come from unfertilized eggs – haploid (one set of chromosomes) ; sperms of each male are identical

Females come from fertilized eggs – diploid (two set of chromosomes) - eggs of each female are 50% identical

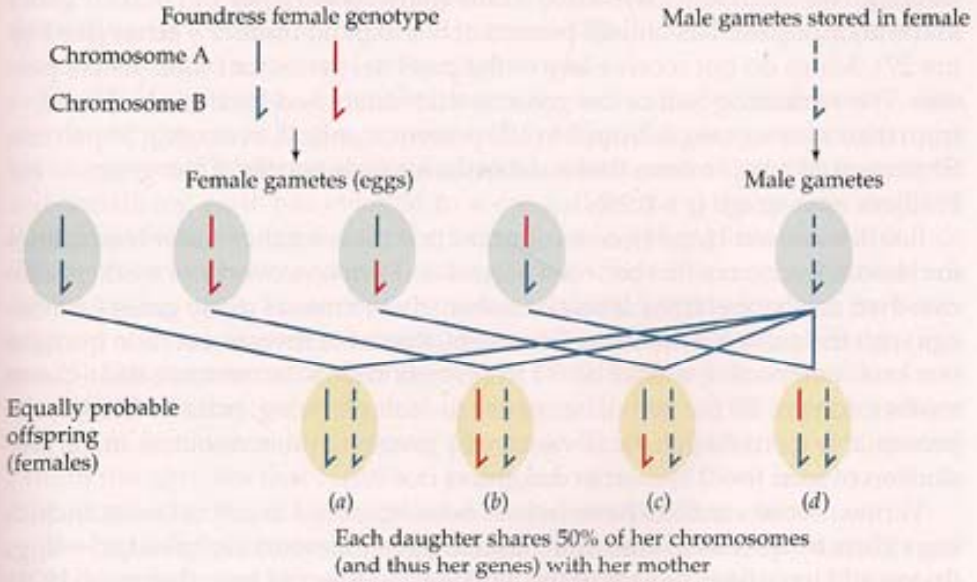
A female mates with a male: all her diploid daughter will carry the same set of paternal genes, but carry 50% of maternal genes

Therefore, **haploidiploid sisters** will share 75% of genes

Helping sisters indeed increase indirect fitness


(A) Mother–offspring genetic relatedness
Foundress female genotype
Male gametes stored in female
Chromosome A
Chromosome B
Female gametes (eggs)
Male gametes
Equally probable offspring (females)
(a)
(b)
(c)
(d)
Each daughter shares 50% of her chromosomes (and thus her genes) with her mother

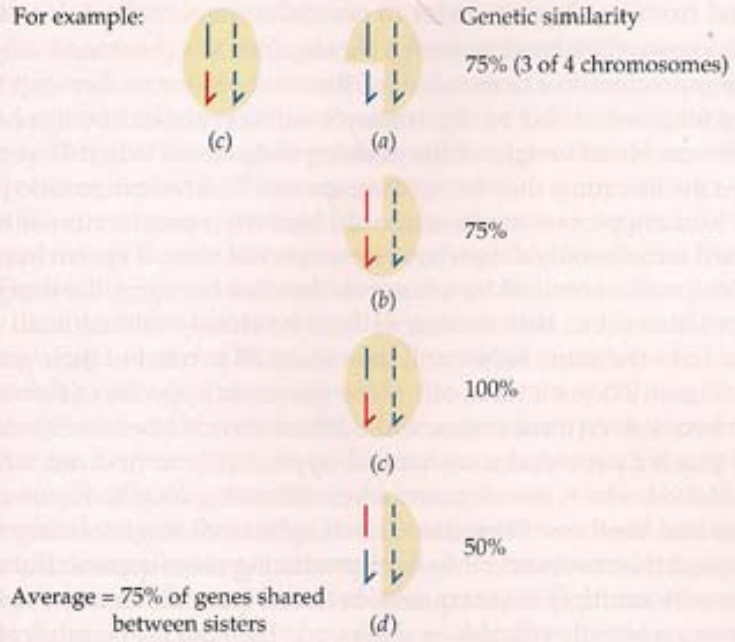
(A) Mother–offspring genetic relatedness



Each daughter shares 50% of her chromosomes (and thus her genes) with her mother

(B) Sister–sister genetic relatedness

Pick any daughter genotype and compare it with the possible genotypes of her sisters



Average = 75% of genes shared between sisters

Sisters help sisters

	Mother	Sister	Daughter	Father	Brother	Son
Haplodiploid						
female	0.5	0.75	0.5	0.5	0.25	0.5
male	1	0.5	1	0	0.5	0.25
Diploid						
female	0.5	0.5	0.5	0.5	0.5	0.5
male	0.5	0.5	0.5	0.5	0.5	0.5

haploidiploid sisters share 75% of genes
diploid sisters share 50% of genes

$$*C \times r_c < *b \times r_b$$

Eusocial females would be expected to prefer to help their mothers raise their sisters, increasing their indirect fitness, rather than concentrating on increasing their direct fitness by raising their own offspring.

How did Eusociality evolve?

1. Kin selection by haplodiploid, r ↑
2. Kin selection by inbreeding, r ↑
3. Ecological (resource) constrains
4. Combination of 1-3.

Naked mole-rats
Eusocial mammals

Naked mole-rats: eusocial mammals

1. Diploid
2. One queen with several kings in a colony
3. Other females as sterile, altruistic workers
4. A lot of inbreeding
5. Why eusocial behavior? Ecological factors?

How did Eusociality evolve?

1. Kin selection by haplodiploid, r ↑
2. Kin selection by inbreeding, r ↑
3. Ecological (resource) constrains
4. Combination of 1-3.


When Queen dies, the worker wasp fights and transforms to the Queen.

How to maintain a social group?

Social dominance hierarchy

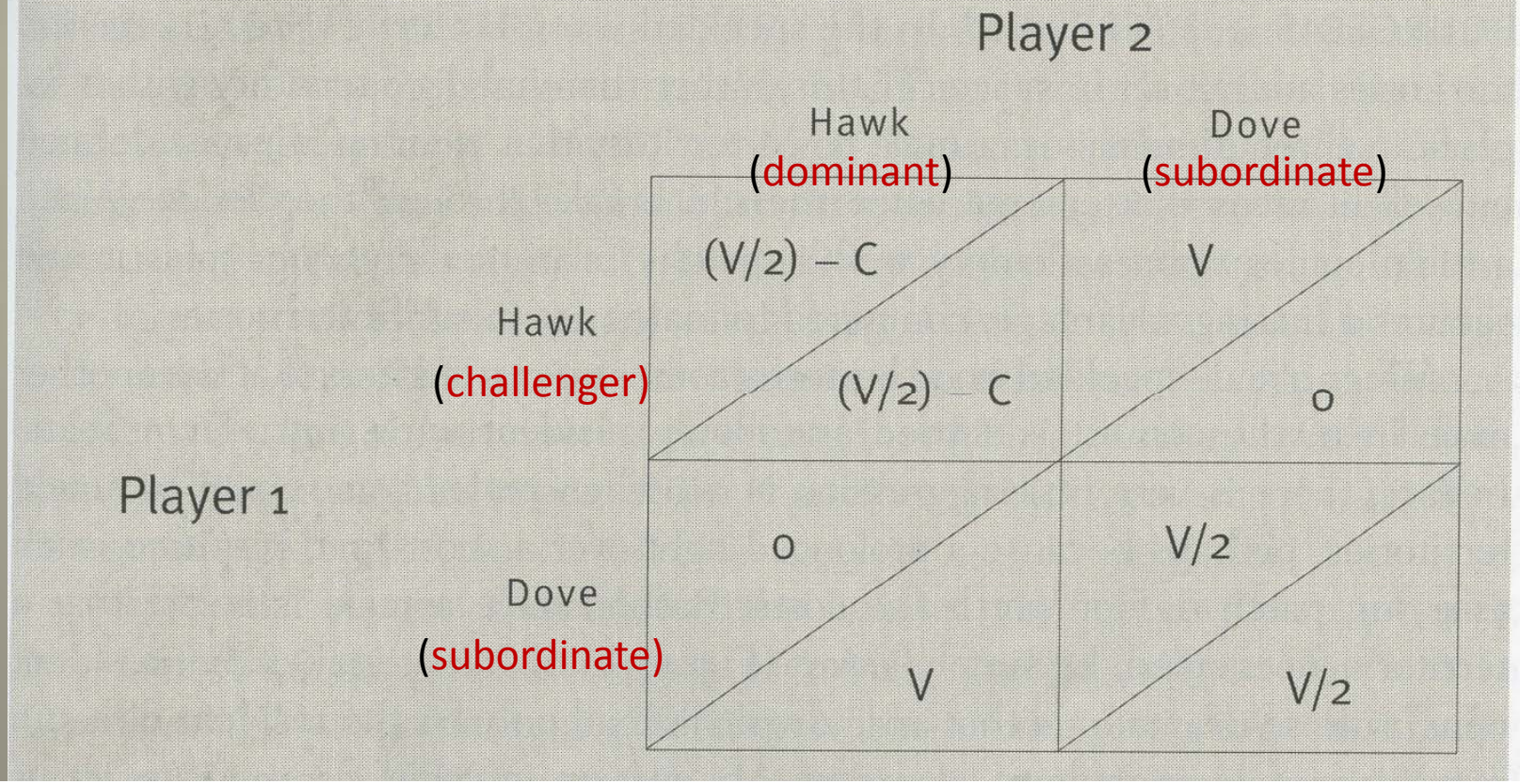
Social dominance hierarchy

Game theory

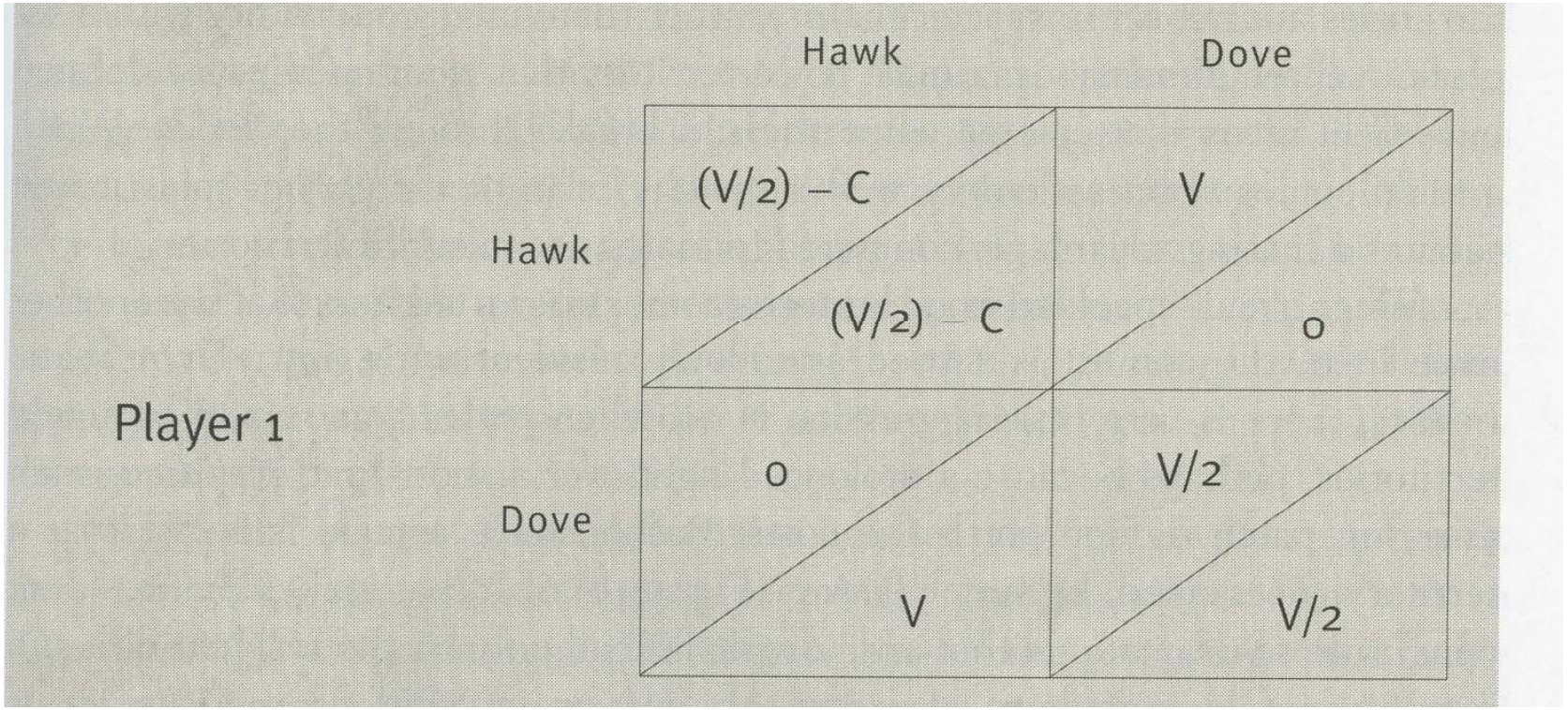
The hawk-dove game

Hawk-Dove game in a social group

TABLE 14.2. The payoff matrix for the hawk-dove game. Both player 1 and player 2 choose between the hawk (always be aggressive) strategy and the dove (bluff, but retreat if opponent escalates) strategy. V = value of resource, C = cost of fighting. Payoffs to Player 1 are shown above the dashed line, and payoffs to Player 2 are shown below the dashed line.



If V> C, then Hawk is an evolutionary stable strategy:
V/2-C >0;
V/2<C (not as good to be a dove)



Bourgeois strategy

Individual to play hawk if it is a territory holder (parents of pied kingfisher)

Individual to play dove if it does not own a territory (offspring helpers of pied kingfisher)

Bourgeois strategy
(Speckled wood butterfly)

M1 (experimentally made a territory owner) always defeated
an intruder male, M2.

If M1 was removed from his territory, M2 occupied it for a while, M1 would now defer to M2

Social status and health

Short term stress of social dominance hierarchy?

During fight-or-flight response (short term stress response):

1. Adrenaline and norepinephrine surge in blood sugar, and oxygen are delivered to the brain, muscles, and heart

2. Non-essential systems, digestive and reproductive system, temporarily shut down

3. Evaluate the cost and benefit of fighting.

Short term effect

Dominant individuals: increased androgen level, more likely to fight than flee.

Subordinate: more likely to flee than fight; have higher circulating levels of glucocorticoid "stress" hormone when going into fights.

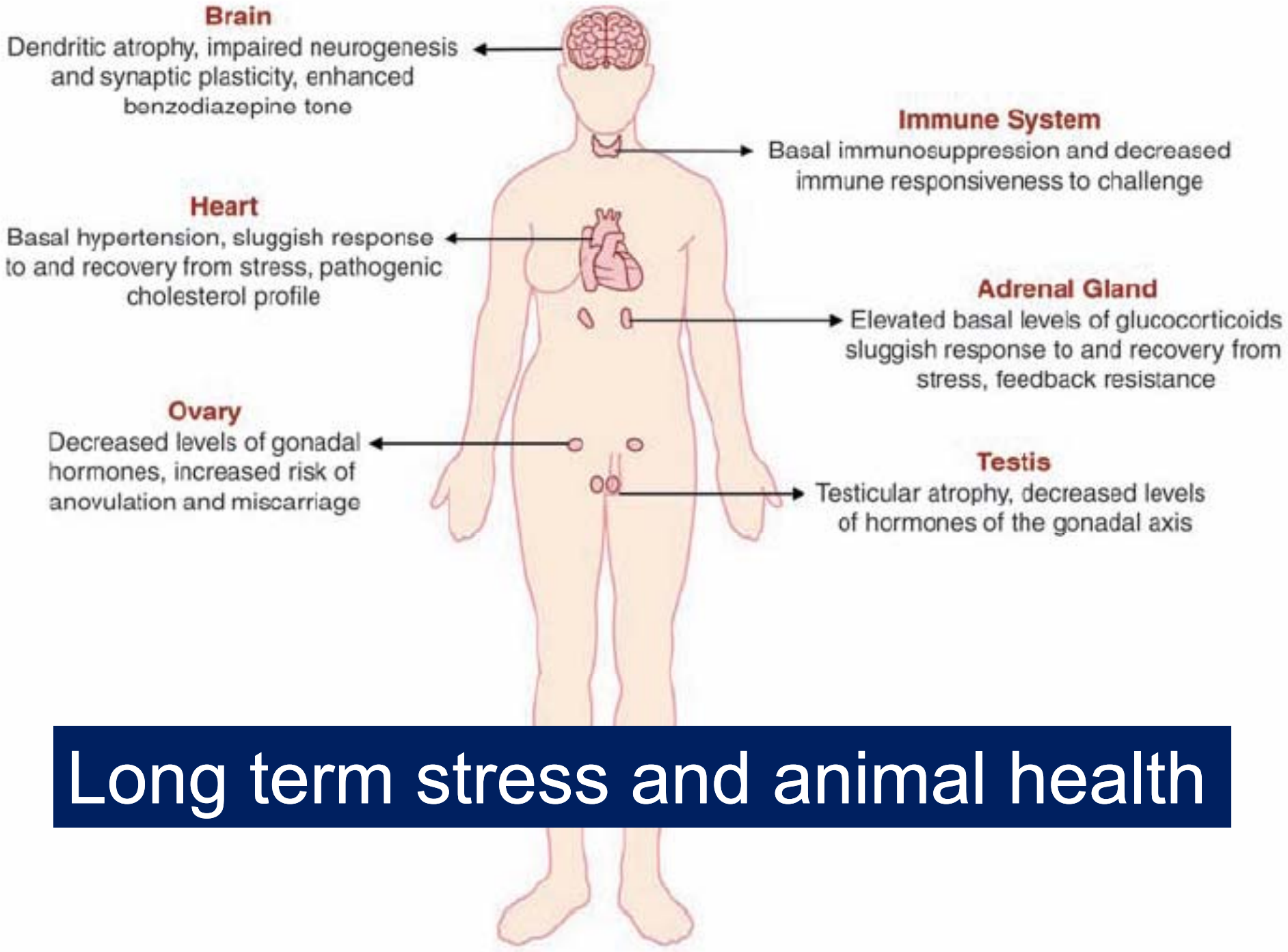
Long term effect?

Stressful social ranks

Higher levels of stress hormones (GC)

Lower immune system against pathogens

Reduced number of synapses;
Reduced number of neurogenesis;
Physical/ mental health deterioate…



Long term stress and animal health

It is not easy to be the dominant one…

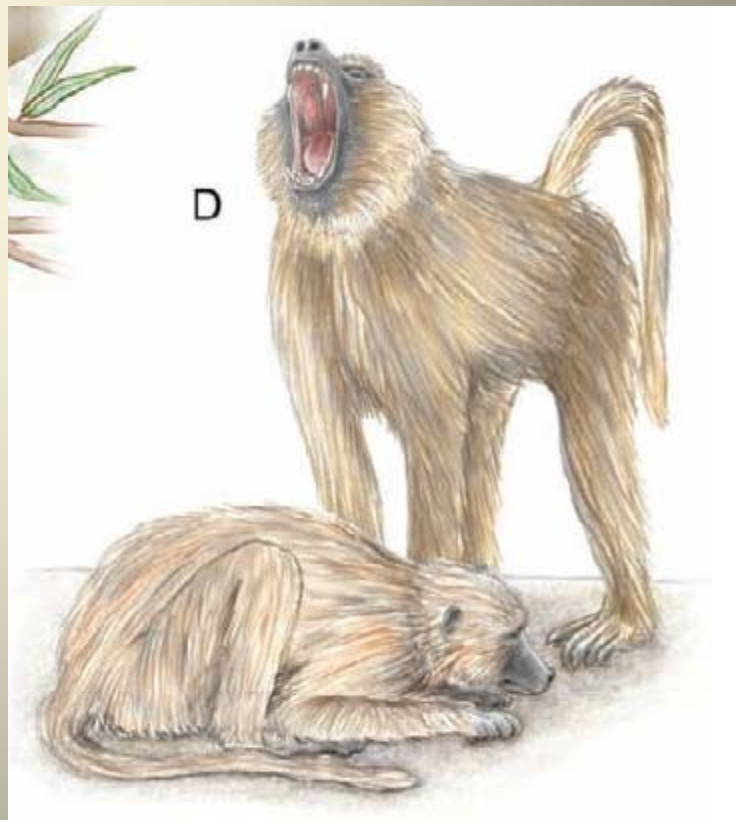
Highly stressful, particularly if

1. Hierarchy is not stable, frequent challenging.
2. Dominance through fight, intimidation.
3. Resource inequity
4. Breeding cycles.

It is not easy to be the subordinate…

Highly stressful if…

1. In a stable hierarchy
2. In male-dominant social hierarchy
3. Less resource inequity



Subordinates cope with stress…

Social support
(grooming, coalition…)

Alternative strategy…
(look like females,
look like juveniles,
wait for opportunity,
Hit and run….)

Human?

Health vs. social ranks?

In humans

Health correlates with socioeconomic status

Psychological stress of feeling poor

Serotonin, aggression and social status

In crustaceans (lobsters)

Increased serotonin →

Enhanced aggression →

Higher social status

Serotonin, aggression and social status

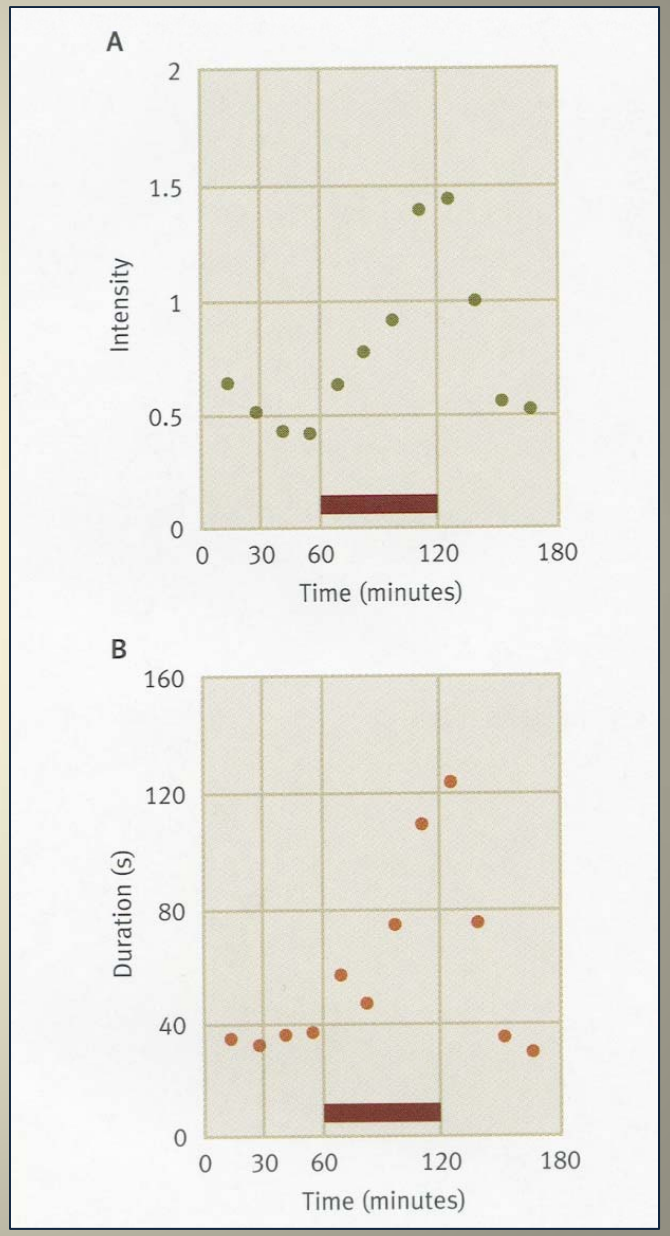
In lobsters

Loser in fights → low serotonin

Avoids aggressive interactions →

Inject serotonin → more aggressive

Inject Prozac (serotonin inhibitor)
→ aggression disappears



Read the following statements about altruistic behavior

1. The family stability of helper-relatives will be greatest in those groups controlling high-quality resources.

2. Help will be expressed to the greatest extent between closest genetic relatives.

3. Replacement mates (stepparents) will invest less in existing offspring than will biologist parents, infanticide may occur

4. Family members will reduce their investment in future offspring after a parent finds a new mate.

5. Decreasing ecological constraints will lead to increased sharing of reproduction.